ANALYSIS OF KNOWN AND NEW HOST RECORDS FOR *PAROXYNA* FROM CALIFORNIA (DIPTERA: TEPHRITIDAE)

RICHARD D. GOEDEN

Department of Entomology, University of California, Riverside, California 92521.

Abstract. — Thirty-seven new rearing records from mature flower heads of Asteraceae are reported for nine of the 19 species of *Paroxyna* now known from California. *Paroxyna coloradensis* Quisenberry is newly reported from California. Hosts remain unknown for seven species and unconfirmed for two species. The host-plant relations for 12 species for which hosts now have been reported are analyzed and compared for the first time. Seven species apparently are monophagous or nearly monophagous, being restricted to a single host genus or known only from one to several, congeneric hosts. Three are oligophagous species reported from more than one host genus in a single tribe. *Paroxyna genalis* (Thomson) appears to be the sole generalist among California species, and is now known from 16 genera and 38 species of host plants representing six tribes of Asteraceae.

The hosts of *Paroxyna* in California represent eight tribes of Asteraceae: Anthemideae, Astereae, Cichorieae, Eupatorieae, Helenieae, Heliantheae, Inuleae, and Senecioneae. The Anthemideae and Eupatorieae are each represented by a single host-plant species for two different monophages. Five California *Paroxyna* spp. may attack only Astereae, the largest of 12 tribes of Astereae in California.

Key Words: Insecta. *Paroxyna*, Tephritidae, Asteraceae, flower-head feeders, host-plant specificities, monophagy

The genus *Paroxyna*, together with the genera Neaspilota, Tephritis, Trupanea, and Urophora, comprise the bulk of the native, nonfrugivorous fruit flies (Diptera: Tephritidae) extant in California (Foote and Blanc 1963, Foote et al. 1993, Goeden 1993, unpublished data). Host plants of California tephritids in the latter four genera were reported, compiled, and analyzed by Goeden (1985, 1987, 1989, 1992, 1993); and Goeden and Blanc (1986) provided an abbreviated account of hosts of two species of Paroxyna. Publication of the handbook on North American Tephritidae by Foote et al. (1993) inspired and facilitated the present analysis of known and new host plants of Paroxyna from California. Because Parox*yna* species are difficult to identify, locate, sample, and study in nature, this analysis of my admittedly meager findings of the past 13 years on the host-plant relations of this genus may otherwise have gone unreported. Companion life-history studies of selected species of California *Paroxyna* eventually will be reported separately beginning with *P. genalis* (Thomson) (Goeden, Headrick, and Teerink, unpublished data).

MATERIALS AND METHODS

Materials and methods used were described by Goeden (1985, 1992). Voucher species of tephritids reside in my research collection; pressed voucher specimens of uncommon or otherwise poorly represented host-plant species were deposited in the Herbarium of the University of California, Riverside.

RESULTS

New rearing records are listed below for eight of 18 species of Paroxyna reported from California by Foote et al. (1993), including P. opacipennis (Foote) transferred by them from *Tephritis* at the suggestion of Jenkins (1985). Paroxyna coloradensis Ouisenberry is newly reported from California. Host records unreported by Wasbauer (1972), Novak (1974), Goeden (1983), Goeden and Blanc (1986), or Foote et al. (1993) are listed by genera and species in the manner of Goeden (1993). All flies were reared from ca. 1-liter samples of mature flower heads. Among multiple samples of a newly reported host-plant species, only the sample from which the most individuals of each fly species were recovered is reported. The plant nomenclature used largely follows Munz and Keck (1959) and Munz (1968, 1974). The insect nomenclature follows McAlpine (1981) and Foote et al. (1993). Rearing records for the flies and their host plants are listed alphabetically.

Paroxyna californica Novak

New host records.—*Arnica chamissonis* Lessing; 6 & and 4 9; Campito Meadow at 3230 m on White Mountain, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Arnica longifolia* deCandolle; 21 & and 15 9; along Deadman Creek at 2800 m, W of Sonora Pass, Stanislaus Nat. Forest, Tuolumne Co.; 8.ix.1988. *Arnica sororia* Greene; 27 & and 42 9; along Deadman Creek at 2500 m, Inyo Nat. Forest, Mono Co.; 9.ix.1986.

Paroxyna clathrata (Loew)

New host genus.-Artemisia.

First known host record.—*Artemisia tridentata* Nuttall; 55 8 and 48 9; SW of Monitor Pass at 2440 m, Toiyabe Nat. Forest, Alpine Co.; 10.ix,1992.

Paroxyna coloradensis Quisenberry

New host genus.-Aster.

First known host record.—*Aster occidentalis* (Nuttall) Torrey and Gray; 1 &; Poison Spring at 2040 m, Stanislaus Nat. Forest, Calaveros Co., 29.vii.1992.

Paroxyna dreisbachorum Novak

New host genus.—*Erigeron*.

First known host record.—*Erigeron peregrinus* (Pursh) Greene: 4 & and 3 &: Kaiser Pass Meadow at 2720 m, Sierra Nat. Forest, Fresno Co.; 17.viii.1988.

Paroxyna genalis (Thomson)

New host genera.—Agoseris, Antennaria, Aster, Chrysopsis, Crepis, Encelia, Grindelia, Lepidospartum, Tetradymia, Venegasia.

New host records.-Agoseris glauca (Pursh) Greene; 10 8 and 12 9; Frenchman Lake at 1700 m, Plumas Nat. Forest, Plumas Co.; 22.viii.1989. Antennaria parvifo*lia* Nuttall: 3 9: Ebbett's Pass at 2630 m. Toivabe Nat. Forest, Alpine Co.; 30.vii.1992. Antennaria rosea Greene, 1 8 and 1 9: N fork of Mission Creek, San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 19.viii.1982. Aster chilensis Nees von Esenbeck; 1 & and 1 9; W of Loleta at 8 m, Humboldt Co.; 2.ix.1987. Aster eatonii (Gray) Howell; 5 8 and 3 9; above Perazo Meadow at 2000 m. Tahoe Nat. Forest, Sierra Co.; 10.ix.1986. Aster occidentalis; 5 & and 8 9; NE shore of Round Valley Reservoir at 1370 m, Plumas Nat. Forest, Plumas Co.; 10.ix.1986. Chrvsopsis breweri Gray; 2 8 and 1 9; Iron Mountain Ridge at 2100 m, El Dorado Nat. Forest, El Dorado Co.: 7.ix.1988. Crepis acuminata Nuttall; 6 8 and 14 9; Mineret Summit at 2800 m. in Mammoth Lakes area, Invo Nat. Forest, Mono Co.; 21.vii.1987. Crepis occidentalis Nuttall; 6 8 and 7 9; along Blue Lake Road at 2480 m, Toiyabe Nat. Forest, Alpine Co.; 30.vii.1992. Crepis rucinata

Torrey and Gray; 1 8 and 1 9; below Boundary Peak on E side of White Mountain at 2440 m, Inyo Nat. Forest, Esmeralda Co., Nevada (just across California border); 26.vii.1989. Encelia californica Nuttall: 1 δ; Carpenteria, Santa Barbara Co., 16.iv.1980. Eriophyllum confertiflorum (deCandolle) Gray; 12 8 and 14 9; along Blue Ridge Road at 2430 m, Angeles Nat. Forest, Los Angeles Co.; 1.viii.1990. Eriophyllum lanatum (Pursh) Forbes: 11 8 and 8 9: SW of Arrowbear Lake at 1800 m: San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 19.vii.1990. Grindelia stricta deCandolle; 6 8 and 8 9; W of Loleta at 3 m, Humboldt Co.; 2.ix.1987. Haplopappus apargioides Gray; 1 9; Upper Sedge Meadow at 2750 m, Invo Nat. Forest, Mono Co.; 18.ix.1991. Haplopappus squarrosus Hooker and Arnott; 1 8; along Kitchen Creek Road at 1300 m, Cleveland Nat. Forest, San Diego Co.; 23.x.1984. Haplopappus venetus (Humboldt) Blake; 1 8 and 1 9; Frazer Point, Santa Cruz Island, Santa Barbara Co.: 8.x.1985. Lepidospartum squamatum (Gray) Gray; 4 8 and 3 9; Central Valley, Santa Cruz Island, Santa Barbara Co.: 9.x.1985, Senecio breweri Davy; 48 8 and 46 9; E of Woody on Doney Hill at 1000 m, Kern Co.; 18.v.1989. Senecio clarkianus Grav: 3 8 and 6 9; Poison Meadows, 16 km from Bass Lake at 2000 m. Sierra Nat. Forest. Madera Co.: 16.viii.1988. Senecio hydrophilus Nuttall: 1 ð and 2 9; Little Walker Cowcamp on Little Walker River at 2010 m, Toiyabe Nat. Forest, Mono Co.; 27.vii.1992. Senecio ionophyllus Greene; 12 8 and 21 9; Upper Aspen Meadow, San Bernardino Nat. Forest (N section), SW San Bernardino Co.: 28. vii. 1987. Senecio mohavensis Gray; 5 8 and 6 9; Box Canyon at 260 m, Riverside Co.: 16.iv.1992. Senecio triangularis Hooker: 327 & and 318 9; Dana Plateau at 3350 m, Invo Nat, Forest, Mono Co.; 8, viii, 1986. Tetradymia canescens deCandolle; 1 ô; 1 km E of Aspen Grove, San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 19.viii.1982. *Venegasia carpesioides* de-Candolle; 26 and 29 9; Jalama Canyon at 100 m, Santa Barbara Co.; 18.iv.1985.

Paroxyna jamesi Novak

New host genus.—Aster.

New host records.—*Aster eatonii*; 1 &; above Perazo Meadow at 2000 m, Tahoe Nat. Forest, Sierra Co.; 10.ix.1986. *Aster* occidentalis; 3 & and 2 9; 6 km W of Sawmill Meadow at 2600 m, Inyo Nat. Forest, Mono Co.; 17.ix.1991.

Paroxyna pallidipennis (Cresson)

New host genus.-Brickellia.

First known host record.—*Brickellia* grandiflora (Hooker) Nuttall; 145 å and 227 9; E side of Ebbett's Pass at 2310 m, Toiyabe Nat. Forest, Alpine Co.; 7.ix.1988.

Paroxyna sabroskyi Novak

New host genus.-Hieraceum.

New host record.—*Hieraceum albiflorum* Hooker: 15 8 and 20 9; N of Bass Lake at 1260 m, Sierra Nat. Forest, Madera Co.; 21.vi.1989.

Paroxyna variabilis (Doane)

New host record.—*Agoseris retrorsa* (Bentham) Greene; 3 & and 2 9; Pinchurst at 1360 m, Lassen Nat. Forest, Shasta Co.; 24.viii.1989.

DISCUSSION

The host-plant specificities of *Paroxyna* species in California apparently are as diverse as those reported elsewhere for *Tephritis* (Goeden 1993) and *Trupanea* (Goeden 1985, 1992) species. All three genera include true monophages, each with a single host-plant species; nearly monophagous tephritid species confined to several host species in one genus; oligophagous species attacking two or more host genera in one tribe; and at least one generalist that attacks hosts from several tribes of Asteraceae (Goeden 1985, 1992, 1993). Host plants remain un-

known for seven species of California occurrence: Paroxyna distincta Quisenberry, P. dupla (Cresson), P. farinata Novak, P. occidentalis Novak, P. opacipennis (Foote), P. pygmaea Novak, and P. steyskali Novak (Foote et al. 1993). Of these seven species, I have swept all but dupla during mid-summer to early fall from flowering shrubs, e.g. Artemisia and Chrysothamnus spp., at higher elevations in our mountains, but still have not located and sampled the mature flower heads of their respective host plants. To date, all eight, reared, described species as well as at least three, possibly undescribed species currently under study are ovule and soft achene feeders as larvae: moreover, some of these species also score receptacles, and presumably, most of them also feed on the sap that collects at their feeding sites in flower heads (Goeden and Teerink, unpublished data). None has been found to form galls: neither facultatively like Trupanea conjuncta (Adams) (Goeden 1987), nor obligatorily like some species of Trupanea (Goeden 1985, 1992) and Tephritis (Goeden 1993).

Among the apparent, true monophages, my rearing record for *P. clathrata* is the first for this common, widespread western species. Previous records for *P. clathrata* from *Haplopappus pinifolius, Senecio douglasii*, and *S. integerrimus* in Goeden (1983) and Foote et al. (1993) refer to misidentified *P. genalis.* As now reported, *P. clathrata* is the only *Paroxyna* known with a host from the tribe Anthemideae (Novak 1974, Foote et al. 1993).

Paroxyna coloradensis also is reported from its first known host, Aster occidentalis, besides being newly reported from California. My single specimen of this distinctive dark species was identified by F. L. Blanc. Moreover, it was reared from a sample collected at an altitude about 1000 m below the "high Rocky Mountain elevations" of 2900 to 3600 m in Colorado and Wyoming which Novak (1974) reported as its distribution. Paroxyna driesbachorum was described as a rare species that occurs in high mountainous areas up to 3800 m by Foote et al. (1993). Novak (1974) described it only from Colorado. It is reported here from Erigeron peregrinus, its first record from California and from its only known host, and as the only species of Paroxyna reared from a host in this large genus in the tribe Astereae. I otherwise have reared only Neaspilota, Procecidochares, Tephritis, and Trupanea to date from among the 11 species of Erigeron that 1 have sampled (Goeden 1985, 1987, 1992, 1993, unpublished data).

Paroxyna murina (Doane) has been reported only from *H. bloomeri* Gray (Novak 1974). However, I have been unable to verify this host record despite my repeated samplings and rearings of *Trupanea*, *Tephritis*, and *Euaresta* spp. from the flower heads of *H. bloomeri* (Goeden 1992, 1993, unpublished data). This unconfirmed host also is in the tribe Astereae, which is the largest tribe of Asteraceae in California (Munz and Keck 1959, Goeden 1992, 1993).

My rearing record for *P. pallidipennis* from *Brickellia grandiflora* similarly is the first reported for this monophage. This is the only Nearctic species of *Paroxyna* reared from a host in the tribe Eupatorieae and from the genus *Brickellia*, which otherwise hosts only *Procecidochares flavipes* Aldrich (Goeden, unpublished data, Foote et al. 1993) and *Trupanca* spp. (Goeden 1992) in California.

Any analysis of host specificities like the above assigning species of phytophagous insects to single host-plant species must recognize that such apparent monophagy may reflect instead the incomplete knowledge of host plants characterizing most native North American, phytophagous insects (Goeden and Teerink 1993). One of my long-term research goals has been to rectify this deficiency for California Tephritidae (Goeden 1983, 1985, 1987, 1989, 1992, 1993, present paper).

Paroxyna albiceps (Loew) was reported

from six species of *Aster* in the tribe Astereae by Novak (1974), none of which occur in California. As this tephritid is known from California (Novak 1974, Foote et al. 1993), its host range presumably includes one or more species of *Aster* other than the 19 species that I have sampled to date (unpublished data). As reported above, I have reared only *P. genalis* and *P. jamesi* from one or more of these 19 *Aster* species to date.

Paroxyna californica is now known from four species of hosts in the genus *Arnica* in the tribe Senecioneae (Foote et al. 1993, present report). The record for *A. sororia* Greene attributed to Goeden (1983) by Foote et al. (1993) is not found in that paper, but instead may refer to an unpublished communication from me. For this reason, I have included my rearing record from *A. sororia* in the present report.

Paroxyna jamesi was reported from Grindelia nana Nuttall by Novak (1974), but 1 have not reared any tephritid from three samples of flower heads of this plant species. However, as reported above, I have reared *P. jamesi* from two species of *Aster*, which also are in the tribe Astereae.

Paroxyna snowi Hering was reported from *Senecio triangularis* (Novak 1974) and *Arnica cordifolia* Hooker (Foote et al. 1993), both in the tribe Senecioneae. 1 have not sampled the latter plant species, and, besides *Tephritis* and *Trupanea* (Goeden 1992, 1993), have reared only *P. genalis* from five samples of the former host to date.

Paroxyna sabroskyi and P. variabilis are two more oligophagous species, i.e. reported from more than one host genus in a single tribe, in California. The former species has been reported from Stephanomeria virgata Bentham (Goeden and Blane 1986) and above from Hieraceum albiflorum, both in the tribe Cichorieae. All three reported hosts of P. variabilis also belong to the Cichorieae. Besides my new record for P. variabilis from Agoseris retrorsa, I have confirmed the reeord for A. grandiflora (Nuttall) Greene, but not the record for Microseris laciniata (Hooker) Shultz-'Bipontinus' in Novak (1974).

Paroxyna genalis appears to be the sole generalist among the California species of Paroxyna. It is now known from 16 genera and 38 species of host plants representing six tribes: Astereae, Cichorieae, Helenieae, Heliantheae, Inuleae, and Senecioneae. The flies that now key to the highly variable ge*nalis* in reality may comprise several, more stenophagous species of Paroxyna, but resolution of this possibility awaits future taxonomic and biological studies. All 38 species of reported hosts occur in California, where only those published host records for Microseris sp. in Novak [1974, as corpulenta (Cresson)] and for Senecio jacobaea L. in Frick (1964) remain unconfirmed. However, both unconfirmed hosts belong to the Cichorieae, from four other species and two genera of which I also have reared P. genalis, so the use of this tribe by this tephritid has been clearly established. Likewise, I have reared P. genalis from 11 additional species of Senecio (Goeden 1983, as clathrata; Goeden and Blanc 1986), while confirming records for three hosts in Foote and Blanc (1963), Frick (1964) or Novak (1974). Senecio jacobaea is an accidentally introduced weed of European origins (Munz and Keck 1959), and thus represents an infrequently encountered example of a native tephritid and endophage successfully transferring to an introduced plant species, presumably from one or more native congeneric hosts. This phenomenon also was documented for Paracantha gentilis Hering from native to introduced Cirsium thistles in southern California (Goeden and Ricker 1986, Headrick and Goeden 1990).

Unlike several *Trupanea* spp. in California (Goeden 1985, 1992), only *P. genalis* and *P. jamesi* are now known to attack the same two, congeneric, plant species. In addition, both tephritids, plus *P. coloradensis*, are now known from one of these hosts. *Aster occidentalis*. This low frequency of intrageneric resource sharing among Califor-

nia Paroxyna probably reflects P. genalis being the sole generalist; whereas Trupanea contains at least six generalists in California (Goeden 1985, 1992), and commensurately, a smaller proportion of monophages than Paroxyna. As noted above, besides the two identical species of Aster shared by P. genalis and P. jamesi, this plant genus also is attacked by P. albiceps and P. coloradensis. Other host genera apparently shared by *P*. genalis include: Agoseris and Microseris with P. variabilis, Grindelia with P. jamesi, Haplopappus with P. murina, and Senecio with P. snowi. The evolutionary significance of these shared host resources is left to my systematist colleagues to ponder (Goeden 1992). Consistent rearings of the same pairs of species from flower-head samples also have provided evidence used to synonymize certain species of *Paroxyna* (Goeden and Blane 1986) and Neotephritis (Goeden et al. 1987).

Acknowledgments

The technical support of D. H. Headrick, G. F. Pratt, D. W. Rieker, and J. A. Teerink is gratefully acknowledged. The botanical expertise of A. C. Sanders, Curator of the Herbarium at the University of California, Riverside, who identified or facilitated identification of all plants mentioned in this paper, is once more acknowledged as being of fundamental help to my tephritid research. F. L. Blanc identified or confirmed my identifications of several species of Paroxyna reported herein, and helped aseertain which still unreported host associations involving possibly undescribed species warranted further attention. I also sincerely thank F. L. Blane, D. H. Headrick, G. J. Steek, and J. A. Teerink for their helpful comments on earlier drafts of this paper.

LITERATURE CITED

- Foote, R. H. and F. L. Blanc. 1963. The fruit flies or Tephritidae of California. Bulletin of the California Insect Survey 7, 117 pp.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993.

Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca and London.

- Frick, K. E. 1964. Some endemic insects that feed on introduced tansy ragwort (*Senecio jacobaea*) in western United States. Annals of the Entomological Society of America 57: 707–710.
- Goeden, R. D. 1983. Initial host-plant records for five species of fruit flies from southern California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 85: 399–400.
- 1985. Host-plant relations of *Trupanea* spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington 87: 564–571.
- 1987. Host-plant relations of native Urophora spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington 89: 269–274.
- 1989. Host plants of *Neaspilota* in California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 91: 164–168.
- . 1992. Analysis of known and new host records for *Trupanea* from California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 94: 107–118.
- —. 1993. Analysis of known and new host records for *Tephritis* from California, and description of a new species, *T. joanae* (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 95: 425–434.
- Goeden, R. D. and F. L. Blanc. 1986. New synonymy, host, and California records in the genera *Dioxyma* and *Paroxyma* (Diptera: Tephritidae). Pan-Pacific Entomologist 62: 88–90.
- Goeden, R. D., T. D. Cadatal, and G. L. Cavender. 1987. Life history of *Neotephritis finalis* (Loew) on native Asteraceae in southern California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 89: 552–558.
- Goeden, R. D. and D. W. Ricker. 1986. Phytophagous insect faunas of two introduced *Cirsium* thistles, *C. ochrocentrum* and *C. vulgare*, in southern California. Annals of the Entomological Society of America 79: 945–952.
- Goeden, R. D. and J. A. Teerink. 1993. Phytophagous insect faunas of *Dicorta canescens* and *Iva axillaris*, native relatives of ragweeds, *Ambrosia* spp., in southern California, with analyses of insect associates of Ambrosiinae. Annals of the Entomological Society of America 86: 37–50.
- Headrick, D. H. and R. D. Goeden. 1990. Life history of *Paracantha gentilis* (Diptera: Tephritidae). Annals of the Entomological Society of America 83: 776–785.
- Jenkins, J. 1985. A revision of the North American *Tephritis* species attacking *Baccharis* with an eval-

uation of morphological characters. M.S. thesis. Washington State University, Pullman, 132 pp.

- McAlpine, J. F. 1981. 2. Morphology and terminology—adults. *In* McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood, eds., Manual of Nearctic Diptera—1. Monograph of the Biosystematics Research Institute 27: 9–63. Agriculture Canada. Ottawa.
- Munz, P. A. 1968. Supplement to a California Flora. University of California Press, Berkeley.
- 1974. A Flora of Southern California. University of California Press, Berkeley.

- Munz, P. A. and D. D. Keck. 1959. A California Flora. University of California Press. Berkeley.
- Novak, J. A. 1974. A taxonomic revision of *Dioxyna* and *Paroxyna* for America north of Mexico. Melanderia 16: 1–53.
- Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology Occasional Papers No. 19, 172 pp.